Racial and heterosis effects of prolificacy traits on complete diallelic crossings between four rabbit breeds

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Four thousand twenty-five observations of three complete diallelic crossings between four rabbit breeds (California, C; Chinchilla, CH; New Zealand, N and Semi-giant, S) were conducted to determine the racial and heterosis effects on prolificacy traits. In the first study, a generalized linear model through the GENMOD procedure of SAS (2007), was applied which considered the race effects (paternal, maternal and their interaction), parity and generation. In the second, a mixed model through the PROC MIXED procedure, also of SAS, was used, which considered the genotype (cross vs. pure) as random and parity and generation as fixed. The BLUPs resulting from the second model were used when calculating heterosis. The indictors total born (TB), born alive (BA) and number of weaned animals (NW) were analyzed. The maternal breed was the only important effect for the TB and BA. Chinchilla breed highlighted with more than seven kids for both measurements. Non-significant positive heterosis was found in the reciprocal crossings CCH-CHC for each trait under study, as in the CN-NC for the NW. Heterosis was negative or null in the other combinations. The use of C as maternal breed is a way to improve the traits TB and BA. Advantages at the heterosis level are obtained with the CH-CHC crossing for all the prolificacy traits studied and with that of CS-SC for the WN. These results show that crossing is an alternative to increase productivity in different rabbit exploitations.

Key words: *diallelic cross, rabbit, prolificacy, heterosis*

The crossing in rabbits, as an alternative for genetic improvement, is a useful via to improve the prolificacy traits through heterosis and complementation among breeds. It is one of the best options to increase the profits of the warren, as a better productivity and adaptation to the environment is achieved with the hybrids (Ponce de León *et al*. 1997). The majority of the authors state that these traits, due to their characteristics, offer higher kindness when improved through the system (Masoero 1980, Montaldo and Barría 1998, García 1999 and Campos 2001).

It is important to consider that the test of diallelic crossings is a standard procedure of genetic research, which is very used for obtaining varied information on the parental population. Thus, different genetic aspects of the progenitor's performance with their different combinations may be assessed.

This procedure is important for taking objective decisions in the different improvement programs, from the identification of superior genotypes and crossings or promising combinations (Ramos *et al*. 2006). For this reason, several authors (Dickerson 1993, Ghosh and Das 2004 and Lessa de Assis *et al*. 2004) consider it as an efficient method for assessing the genetic and heterotic potential of the different breeds or lines.

The objective of this study was to determine the racial and heterosis effects on prolificacy traits in diallelic crossings of four rabbit breeds in order to have alternatives to increase productivity in different rabbit exploitations through crossing.

Materials and Methods

In order to determine the racial and heterosis effects on prolificacy traits (TB, BA and WN) the reproductive information (4725 observations) of three complete diallelic experiments between four rabbit breeds present in Cuba (California, Chinchilla, New Zealand and Semi-giant) was used, described by Ponce de León *et al*. (1997). The experiments were conducted in San Jose de las Lajas municipality, Mayabeque province, Cuba.

For the matings, in each of the three experiments, breeders and sires from the basic herd were selected, representing the racial genofond under study. The pure sires selected had the fenotypical characteristics of the breed. The multiparous females had normal fecundity and prolificacy parameters (Riverón *et al*. 2003), and the young females had a good physical shape.

The mating design (table 1) was conducted according to the facts of a complete diallelic crossing (4 x 4), according to the states of Griffing (1956 a and b) for the design 1 (diallelic crossings that test self-fecundations, the crossings F1 and the reciprocal, appart from the presence of known maternal effects) and under the structure of a completely randomized design.

The females of each breed were divided into four mating groups. One for mating with sires of the same breed and others with three sires of the resting breeds. The groups were distributed in the pen randomly. Each breeder of each racial group was mated with a different sire, thus, each sire was assigned several females, each of different breed. The sires mated females from different genotypes (pure or crossed), allowing the maximization of the genetic variability.

The different parturitions of each female came from different sires of the same breed in order to have a representability of parity. The management of the matings was conducted by the same personnel in each generation, so the results were not affected by this effect.

Table 1. Mating design and number of observations used in a diallelic cross of four breeds

Maternal breed	Paternal breed				
	California	Chinchilla	N. Zealand	Semi-giant	Total
California	1179.0	70.0	82.0	97.0	1428.0
Chinchilla	89.0	311.0	78.0	86.0	564.0
N. Zealand	66.0	55.0	1076.0	95.0	1292.0
Semi-giant	89.0	62.0	92.0	1198.0	1441.0
Total	1423.0	498.0	1328.0	1476.0	4725.0

The mating was natural and was conducted from the 11 d post-partum during the early hours of the morning, once the heating stage of the breeder was verified. The palpation to verify gestation was carried out at 14-15 d after the mating. Wood nests with bed of wood residues were placed in the pens three days before the parturition. The day of the parturition, when it was presented, the alive and dead animals were counted. The sum of both groups was considered as the total litter.

The animals of the experiments 1 and 2 consumed pelletized feedstuff *ad libitum*, based on cereales, with 18 % CP and green forage of alfalfa (*Medicago sativa*) or ramie (*Boehmeria nivea*). Those of the experiment 3 were supplied commercial feedstuff as meal (17-18% CP, 10-10.8 MJ DE/kg DM and 10-11% CF). The feedstuff was mixed with wheat bran at the time of the supplement. The offer was made so to represent at about 70 % of the requirement according to the category (Lebas *et al*. 1986). Additionally, grass forages were offered *ad libitum*, mainly of king grass (*Pennisetum purpureum*).

The racial effects and heterosis were determined for the prolificacy traits, total born (TB), born alive (BA) and number of weaned animals (NW). The statistical software Statistical Analysis System (SAS) for Windows, version 9.1.3 (2007) was used for the analyses.

Due to their characteristics, the three prolificacy traits under study were discreet variables with Poisson distribution, showed with the distribution analysis test of the software.

A generalized linear model was applied to determine the influence of the different racial effects, with the help of PROC GENMOD of this software. The link function used in this model was the log, proper for distribution of the data under study.

The racial effects of the paternal and maternal genotypes were analyzed in the model, with four types each (California, Chinchilla, New Zealand and Semi-giant), as well as the interaction paternal x maternal genotype, with 16 classes included. The parity effects were also considered (from 1 to 5) and three generations:

$$Y_{ijklm} = \beta_0 + p_i + m_j + (p^*m)_{ij} + n_k + g_l + e_{ijklm}$$

Where:

Y_{ijklm} = f(μ) expected fenotypical value of the character under study according to the function of specific link.

β_0 = intercept; β= vector of unknown parameters associated with the model effects.

p_i = efect of the i-th paternal breed (i=1, 2, 3, 4)

m_j = efect of the j-th maternal breed (j=1, 2, 3, 4)

$(p^*m)_{ij}$ =effect of the interaction between the i-th paternal breed and the j-th maternal breed (ij=1, 2, 3, …,16)

n_k = effect of the k-th parity (l=1, 2, 3, 4, 5)

g_l =effect of the l-th generation (m=1, 2, 3)

e_{ijklmn} = random error associated with the observations are common effects, with mean = 0 and σ_e^2

A mixed model was applied when determining heterosis with the help of PROC MIXED, which considered the effects of genotype, parity and generation. The random effect of genotype was that of Crossings vs Pures:

$$Y_{ijkl} = \mu + g_i + \alpha + \beta_k + e_{ijkl}$$

Where:

Y_{ijk} = fenotypical value of the character under study

μ= populational mean

g_i = random effect of the i-th genotype (i=1, 2)

α_j = effect of the j-th parity (j=1, 2, 3, 4, 5)

β_k = effect of the k-th generation (k=1, 2, 3)

e_{ijkl} = random error associated with the observations with mean = 0 and σ_e^2

This model was applied to the ten databases made from the total data, including the information of reciprocal crossings and that of pure paternal breeds. The best linear unbiased prediction (MPLI /BLUP), resulting from the database processing were used in the following classic formula for calculating heterosis:

$$\text{Heterosis of F1 (\%)} = \frac{\left(\frac{AB+BA}{2}\right) - \left(\frac{A+B}{2}\right)}{\left(\frac{A+B}{2}\right)} \times 100$$

$\left(\frac{AB+BA}{2}\right)$ is the BLUP average of both reciprocals

$\left(\frac{A+B}{2}\right)$ is the BLUP average of both pure breeds

Results and Discussion

Racial effects. The analysis of variance of this group (table 2) showed the maternal breed as the only significant genetic effect. The other effects were not important for the number of weaned animals.

Out of the four maternal breeds under study,

Table 2. Analysis of variance (Chi-square) for the prolificacy traits

Variation source	gl	Prolificacy (Number of animals)		
		TB	BA	WN
Paternal breed	3	3.69	3.82	0.55
Maternal breed	3	9.68*	8.62*	1.85
Paternal breed x maternal breed	9	5.02	6.01	8.12
Parity	4	9.69	10.39*	6.58
Generation	2	202.13***	143.12***	27.11***

* $P < 0.05$ *** $P < 0.001$

Chinchilla, with more than seven kids, advantaged California and New Zealand breeds, for the traits total born and born alive (table 3). The Semi-giant breed had an intermediate performance between the maternal breeds previously mentioned.

In a similar study, Ponce de León and Menchaca (1985) obtained different results of those of this study because the paternal breed was the most important genetic effect, when affecting the born alive and the weaned animals. However, the maternal breed did not influence on these prolificacy traits and the interaction affected only the total born animals. The results of this investigation do not coincide either with those reported by Matheron and Rouvier (1978), who proved that the interaction of the paternal and maternal breeds did influence on the number of weaned animals. The fact that these two studies do not correspond with the results of this, could be due to the statistical method determined and the number of observations.

García (2005) in an incomplete diallelic experiment between five rabbit breeds (the four used in this study and the Cuban breed) found the maternal breed as the most consistent effect, as it influenced on all the prolificacy traits (TB, BA and WN). This result and the present are consequent with that reported in the literature, as the number of animals of a litter at born, depends mainly on the proper characters of the female, or on the mean effect of the dam's genes.

These variations of the effects significance could be due to the great variability of the litter size, influencing certainly the feeding and management conditions. However, the values reached by each maternal breeds under study for the total born, born alive and weaned animals are higher than those obtained in previous studies, conducted in the same facilities by Ponce de León *et al*. (2002) and Ponce de León *et al*. (2003). In the tropics, the small size of the litter at born is frequent, demonstrated by recent studies of Fayeye and Ayorinde (2008) in commercial warrens of Nigeria, where the values of born animals were between 4 and 4.7 kids, inferior to those of this study.

Heterosis. Heterosis for the traits under study is shown in table 4. Considering the presence of heterosis, when the average of crossed animals is different from the mean of the two pure parental breeds (Shull 1914), no significant heterosis values were reached for any of the combinations studied. Only the crossed genotypes CCH-CHC had a superior performance to that of the pure California and Chinchilla for all means, with heterosis values between 1.64 and 6.77 %. The CS-SC, with 3.07 %, also showed better performance than that of their progenitors for the NW indicator. In the cases of reciprocal crossings, with negative heterosis values, it did not reach 6 %.

The positive heterosis values that did not reach the significance are in correspondance with the reports of Falconer and Mackay (1996), who refer that not all the crossings cause an heterosis useful for the improver, and, if the character measurement

Table 3. Number of total born and born alive animals, according to the maternal breed

Maternal breed	NT (No.)	NV (No.)
	Media	Media
California	1.92^{a}(6.8)	1.88^{a}(6.5)
Chinchilla	2.00^{b}(7.4)	1.96^{b}(7.1)
New Zealand	1.93^{a}(6.9)	1.89^{a}(6.6)
Semi-giant	1.96^{ab}(7.1)	1.92^{ab}(6.8)
SE±	0.02	0.02

^{ab}Parameters with different superscripts differ at $P < 0.05$ (Kramer 1956).
( ) original means obtained through identity function.

Table 4. Heterosis (%) calculated for prolificacy traits of the crossings F1 studied.

Crossings		TB (No.)		BA (No.)		WN (No.)	
		Media	SE ±	Media	SE ±	Media	SE ±
CCH- CHC	Intercept	6.14	0.16	6.10	0.14	4.89	0.22
	Pure BLUP	-0.08	0.12	-0.05	0.09	-0.16	0.19
	Crossing BLUP	0.08	0.12	0.05	0.09	0.16	0.19
	Heterosis (%)	2.64	1.64	6.77			
CN- NC	Intercept	6.05	0.23	5.99	0.22	4.88	0.10
	Pure BLUP	0.18	0.21	0.18	0.20	0.00	0.00
	Crossing BLUP	-0.18	0.21	-0.18	0.20	0.00	0.00
	Heterosis (%)	-5.77	-5.83	0			
CS- CS	Intercept	5.97	0.10	5.92	0.22	4.63	0.16
	Pure BLUP	0.00	0.00	0.01	0.04	-0.07	0.11
	Crossing BLUP	0.00	0.00	-0.01	0.04	0.07	0.11
	Heterosis (%)	0.00	-0.34	3.07			
CHN-NCH	Intercept	6.40	0.12	6.24	0.16	5.10	0.18
	Pure BLUP	0.00	0.00	0.07	0.11	0.10	0.14
	Crossing BLUP	0.00	0.00	-0.07	0.11	-0.10	0.14
	Heterosis (%)	0.00	-2.22	-3.85			
CHS-SCH	Intercept	6.03	0.15	5.92	0.17	4.86	0.16
	Pure BLUP	0.00	0.00	0.05	0.09	0.00	0.00
	Crossing BLUP	0.00	0.00	-0.05	0.09	0.00	0.00
	Heterosis (%)	0.00	-1.34	0.00			
NS-SN	Intercept	6.28	0.10	6.17	0.11	4.99	0.11
	Pure BLUP	0.00	0.00	0.00	0.00	0.00	0.00
	Crossing BLUP	0.00	0.00	0.00	0.00	0.00	0.00
	Heterosis (%)	0.00	0.00	0.00			

is the only assessment criterion, the crossing is not useful, unless the reciprocals mean in population F1 is better than the average of both parental breeds. Lobera (2005) pointed that when genetically different lines are selected, but with similar productivity, a better crossing than that of the original lines may be expected, although in the crossing, the heterosis is null or low at levels of particular traits. This would correspond to the exploitation of the complementary between lines.

The heterosis of CCH-CHC, for the traits TB and BA, is between 1.64 and 2.64 %, therefore they are inferior to the range from 6 to 14 %. This was elaborated by Folch (2006), from a review of studies on genetic improvement in rabbits conducted by different authors.

Ponce de León (1977) estimated the heterosis for each reciprocal pair F1 in traits of the litter size of a factorial crossing of four breeds and obtained contrary results to those of this study, as the CCH-CHC crossing had negative heterosis values. Explaining these changes on the crossing performance is not easy. The different performance of the crossings with the *ad libitum* pelletized feeding of the animals could have influenced. The genetic differences attributed to the sampling of the pure breeds for producing the F1could have also influenced.

The results obtained by Ponce de León and Menchaca (1985) evidenced negative heterosis for the reciprocal crossing CCH-CHC for the three traits analyzed and significantly negative for the total born, born alive, for the CN-NC combination. Like in this study, the majority of the other crossings also had non-significant negative heterosis, but with superior values to those of this research.

García *et al*. (2010) calculated heterosis for 10 crossing groups in a complete diallelic one between five breeds. The group CCH-CHC was the only one that showed positive and significant heterosis, for the TB and BA, with values over 5 %.

The reciprocal crossing CN-NC is the commercial cross most used worldwide. The majority of the improvement programs use these lines through the maternal line to obtain the terminal female and take advantage of the heterosis of the reproductive characters (Santacreu 2002 and Roca 2008).

In respect to the heterosis values, the results of this study coincide with those of Ponce de León

(1977), who obtained negative heterosis values for the reciprocal crossings CN- NC. Both results differed from the 10.5 % informed by Lukefahr *et al*. (1983) for this same reciprocal crossing in total born. Likewise, they are different from that referred by Nofal *et al*. (1996), when assessing seven racial groups, included the cross NC. These authors found null heterosis for this mating for the total born and of 4.3 % for the born alive.

According to the results described, it may be concluded that Chinchilla breed, as maternal genotype, is a way to improve the traits of total born and born alive, while with the CCH-CHC crossing, advantages at the heterosis level are obtained for all the prolificacy traits studied and with the CS-SC for the NW, being an alternative to increase productivity through the crossing under different rabbit exploitations.

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